

LETTERS TO THE EDITOR

TOWARDS A PHYLOGENETIC SYSTEM OF GASTROPODA PART I: TRADITIONAL METHODOLOGY—A REPLY

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ABSTRACT

Bieler (1990) provides a critique of the methodology of a phylogenetic analysis of the Gastropoda by Haszprunar (1988). His criticism of an incomplete and inconsistent presentation of character-states and methodology is answered by explaining by examples the way in which the character analysis and the construction of the cladogram were done. I argue that any maximum parsimony analysis with equal weighting of characters will fail to produce the "true" phylogeny because of the high degree of parallelism and convergence within the group. The method presented applies *a priori* criteria for estimating the probabilities of homology and apomorphy (i.e. significance) of characters and constructs the cladogram according to that significance. In the proposed classification, higher taxa are thought to reflect stem-lines of high probability.

Key words: Gastropoda, systematics, classification, phylogeny, cladistics, critique.

INTRODUCTION

Bieler (1990) gives a critique of the methodology of the recently published phylogenetic analysis of streptoneuran Gastropoda by Haszprunar (1988) from a strictly cladistic point of view. Here I want, first, to correct certain points of the original paper (Haszprunar, 1988; cf. appendix); second, to explain briefly the reasons that the analysis was not done by application of accepted cladistic methodology; and third, to provide significant examples of the way in which I weighted the characters and did the analysis. Doing the latter, I accept the major points of Bieler's (1990) critique—no one is perfect.

Thus, I agree with Bieler (1990) that for any "scientific question, it is an integral part of any study to present the data unambiguously, to employ reproducible methods, and to offer testable hypotheses." Maybe I have underestimated the difficulty of following my arguments. I therefore wish at least to show the principles.

PRESENTATION OF DATA

Bieler (1990) is correct in assuming that my analysis was not done by computer, because

during the original study adequate hardware to run phylogenetic software was unavailable. Since then, adequate hardware has become available, and I have become familiar with the advantages and disadvantages of programs like PHYLIP, PAUP and in particular HENNIG'86.

Admittedly there are some mistakes in the text, tables and figures, all of which are of minor importance, however. Nevertheless, I welcome this opportunity to correct those of which I am aware.

Bieler (1990) criticized the fact that I did not provide a comprehensive data-matrix. The way in which I did the analysis, however, does not require a data-matrix (see below), and the main results of the character-analysis have been presented (Haszprunar, 1988: table 2).

THEORETICAL CONSIDERATIONS

Character analysis is the basis of any phylogenetic analysis. Typically plesiomorphic versus apomorphic states are estimated by application of the rules of Hennig (1966) such as outgroup-comparison, data on fossils, ontogenetic sequences, and the like. Often, however, there is no clear outgroup available

(e.g. Houbbrick, 1988; Reid, 1989), and the use of fossils and ontogenetic data has been criticized (Alberch, 1985).

The problem of homology, i.e. the problem of the frequency of change from plesiomorphic to apomorphic character state during phylogeny, seems to be overcome by application of a "maximum-parsimony" analysis, whether by hand or by computer. The working hypothesis of parsimony minimizes the number of analogies (homoplasies) and can produce one (or many) "most parsimonious" tree(s). Colless (1983) has pointed out that the principle of parsimony, which is an operational concept rather than an empirical fact of evolution, does work with negligible rates of failure only if the probability of change in each character-state is very low. As outlined by Gosliner & Ghiselin (1984) for primitive opisthobranchs and identified by Davis (1989) in the Hydrobiidae and in my work on the streptoneurans, however, there is a very large degree of convergence, that is, parallelism, in the data. With an increase in the number of taxa the degree of homoplasy increases (Sanderson & Donoghue, 1989), moreover, suggesting a more or less constant rate of homoplasy among taxa. Indeed, the necessity of a parsimony analysis implies that the basic data matrix is controversial with respect to its proposed synapomorphies. Accordingly, the problem of homology cannot be overcome by parsimony analysis.

The recent cladistic study (done with PAUP) of the Littorinidae by Reid (1989) also shows many cases of homoplasy. Indeed, "59.2% of the character state changes could be ascribed to homoplasy" (Reid, 1989: 59), and this is logically a minimal ("most parsimonious") estimate. Significantly, a final cladogram that differs in certain points from the consensus tree is preferred because "some character-state reconstructions are more likely than others" (Reid, 1989: 63). As stated (Haszprunar 1988: 399), the main problem of any phylogenetic study is that of homology.

As reviewed by Riedl (1975, 1978), Ruppert (1982) and Neff (1986), *a priori* criteria for inference of homology have been provided by Remane (1952, 1954). More recently, Rieger & Tyler (1979, 1985; see also Westheide & Rieger, 1987; Tyler, 1988) have formulated criteria for the counter-version, i.e. the estimation of convergence. Both sets of criteria should be applied to any analysis (see below).

I want to stress that both types of character analysis (homology *versus* analogy, apomor-

phy *versus* plesiomorphy) must be done prior to construction of the tree, and that both are principally inductive by application of the criteria of Remane (1952) and Hennig (1966) among others. Accordingly, each proposed synapomorphy includes a two-fold degree of probability, one with respect to apomorphy ("apo-"), and one with respect to homology ("syn-") (Haszprunar, 1989). In the case of character-states, even two analyses of homology are necessary: first, whether all the states belong to the same (homologous) character; secondly, with respect to the homology of the advanced state. For example, in an analysis of the gills of gastropod groups and in particular the (plicate) gill of primitive opisthobranchs, two questions of homology must be answered (for detailed discussion, see Haszprunar, 1985: 20–21; Haszprunar, 1988: 382): (1) Is the opisthobranch gill a homologue of the prosobranch gill (i.e. a ctenidium)? (2) If so, is the plicatid gill homologous in all opisthobranchs?

I believe that these probabilities must be used to "weight" the characters used in the analysis. In other words, the "weight" is not a feature of the character itself, but the degree of likelihood in the present analysis (cf. also Bryant, 1989).

There is no escape from the weighting of characters. Also, the usual analysis involving maximal parsimony weights characters by selecting them (characters not selected lack weight) and by giving each selected character equal weight. Insofar as the degree of homoplasy is great, differentiated weighting of selected characters becomes essential, however. Although Remane (1952) has indicated the way to infer distinct probabilities for a proposed homology, there is still no clear procedure for quantitative *a priori* weighting of characters (e.g. Neff, 1986; Westheide & Rieger, 1987; Bryant, 1989). In using computer algorithms, one possibility would be to include in the analysis only characters with high significance; another is to establish a system of differential weighting (e.g. 1/3/5 corresponding "low/ medium/ high" significance).

These considerations shed light on data presentation as well. For instance, the frequency and circumstances of transformation of coiled shells into asymmetrical limpet-like ones are unimportant; the statement "many" shows that the significance of this character is very low in this phylogenetic analysis. (Its significance might be high in another one, however.)

PRACTICAL CONSEQUENCES

General Remarks

In this section I wish to show by examples the way in which the character analysis and the construction of the cladogram were done in the original paper. For character analysis, I have selected two examples, the number of gills and the conditions of the anterior nerve ring, the significance of which differ considerably. These significances are estimated prior to construction of any cladogram by application of the rules of Remane (1952), Rieger & Tyler (1979, 1985), Neff (1986), Westheide & Rieger (1987) and Tyler (1988). Two groups, Neritimorpha and Pyramidelloidea have been selected to demonstrate the construction of the cladogram.

It was assumed *a priori* that the taxa used in the study all were holophyletic (i.e. monophyletic *sensu* Hennig, 1966), implying that changes within a taxon are secondary phenomena. This approach also concerned the Euthyneura the holophyly of which has been shown earlier (Haszprunar, 1985a,b). It will be shown that in one case (Allogastropoda) this assumption did not work and necessitated the consideration of the subtaxa (see below).

Number of Ctenidia

The question of ctenidial homology throughout the gastropods has been discussed at length by Haszprunar (1985a: 20–22; 1988: 377–383). Whereas the gills of Cocculiniformia, of Valvatoidea, of the allogastropod groups and the Euthyneura were considered to be secondary structures, the gills of the remaining streptoneuran groups were assumed to represent homologues.

Outgroup comparison (Cephalopoda, Tryblidiida) makes it nearly certain that the presence of paired pallial organs is the primitive condition among gastropods. This conclusion is supported by the facts that even gastropods with two gills often have reduced the right one, and that in the Trochoidea and Lepetodriloida the blood supply of the right gill is retained although the gill itself has been lost. The probability for the hypothesis "plesiomorphy: two ctenidia; apomorphy: one (left) ctenidium" is therefore very high.

Next the probability was considered whether the change from two ctenidia to one occurred once or often in gastropod evolution.

Two functional gills are present only in vetigastropod groups ("zeugobranchs"), and even within this group two subgroups have lost the right ctenidium. Anatomical features in Neritimorpha, in which most species have a diotocardian heart and certain species even have a gill-rudiment (Fretter, 1965) and Docoglossa—Patellidae (with two osphradia) likewise suggest an original condition of two ctenidia in these taxa.

Functional morphology shows that a change from two to one ctenidium results in advantages for the animal with respect to water currents in the mantle cavity (Yonge, 1947). Indeed, the presence of two ctenidia necessitates a slit or hole(s) in the shell for passage of waste. Finally, because in zeugobranch gastropods, such as *Haliotis*, the left ctenidium is formed first in ontogeny (Crofts, 1937), a heterochronic process might easily result in a loss of the right ctenidium.

On the whole, I concluded that the change from two to one (left) ctenidium probably occurred several times in gastropod evolution. Thus the probability of the respective synapomorphy, i.e. the probability of the homology of the change from plesiomorphic to apomorphic condition, is low.

Anterior Nervous System

The homology of the main ganglia of the anterior nerve ring in gastropods is well established by identical relative positions and interconnections and by identical fields of innervation.

Among the Streptoneura, two conditions of the anterior nerve ring with respect to the relative position of the ganglia can be distinguished: the pleural ganglion might be close to the pedal one (hypoathroid condition) or close to the cerebral one (epiathroid condition). Outgroup comparison is unsatisfactory, because the Tryblidiida lack pleural ganglia and the Cephalopoda have a highly concentrated nervous system. Ingroup comparison reveals, however, that the hypoathroid condition is generally correlated with other plesiomorphic characters, such as presence of nares, paired pallial and excretory organs, or external fertilization. The hypothesis "plesiomorphic: hypoathroid condition—apomorphic: epiathroid condition" therefore appears well founded.

Again it is now necessary to estimate the number of changes from the hypo- to the epiathroid condition. There is not a single strep-

toneuran taxon in which a mixture of the two conditions occurs (for Viviparidae cf. Haszprunar, 1988: 395). In addition, the distribution of both character states is largely correlated with the ability to produce planktotrophic larvae (exception: certain Neritoidea). On the other hand, a selection pressure that could force such a change is unknown. Moreover, both conditions are unaffected by concentration of the nervous system. Summarizing the argument, I assumed the syn—apomorphy "epiathroid nerve ring" to be of very high significance for streptoneuran phylogeny.

Position of Neritimorpha

Based on the results of the character analysis, estimation of the systematic position of the Neritimorpha starts with consideration of the characters with the highest significance, such as the hypoathroid nervous system.

This step alone reduces drastically the number of possible trees. Starting the analysis with 28 taxa (Haszprunar, 1988: fig. 5) 1.6×10^{35} trees are possible. Accepting "epiathroid nervous system" as a synapomorphy leaves 18 taxa and thus 6.3×10^{18} possible trees [$\times = (2n-3)!/2^{(n-2)}(n-2)!$; in which n is the number of taxa].

Among those "Archaeo-" gastropods, there are two sequences of radular types, each of them again with high significance (stereoglossate—flexoglossate; rhipidoglossate—taenioglossate; Haszprunar, 1988: 390–391). This places the Docoglossa (= Patellogastropoda) and hot-vent group C below and the architaenioglossate groups above the Neritimorpha. The number of possible trees involving the Neritimorpha is further reduced to 3.2×10^{11} (13 taxa remain). Upon consideration of the distribution of ctenidial skeletal support (Haszprunar, 1988: 377–381), *Neomphalus*, the Vetigastropoda and the Seguenzioidea are placed above the neritimorph clade. The number of possible trees is now 15 (4 taxa remain). The Cocculiniformia share many plesiomorphic characters with the Docoglossa, including the primary limpet shell (Haszprunar, 1988: 370–372); thus they are grouped below the Neritimorpha. Finally, *Melanodrymia* shares several characters, such as radula type and protoconch features, with *Neomphalus* and the Vetigastropoda, and is therefore placed above the neritimorph offshoot.

This solution agrees with several character sequences of high significance. The assump-

tion that the Neritimorpha belong among the higher gastropods is based, however, on character stages each of which is correlated with reproductive biology, namely internal fertilization and planktotrophic veligers. The probability of convergent evolution of the features of neritimorph reproductive biology is very high: first, details of the respective characters differ considerably between Neritimorpha and higher groups (genital system, sperm structure, protoconch features); and second, there are numerous examples of internal fertilization within other archaeogastropod clades, and larval planktotrophy has been established through parallel evolution among the Bivalvia.

Position of Pyramidelloidea

Again, the analysis begins with consideration of neural conditions. Earlier the Pyramidelloidea were placed together with the Architectonicoidea in a clade called Allogastropoda (Haszprunar, 1985a). The epiathroid condition of the anterior nerve ring placed the Allogastropoda among the "Apo-"gastropoda, the lack of parietal ganglia and the retention of (at least osphradial) streptoneury (Haszprunar, 1988: 394) suggest a grouping of the Allogastropoda below the euthyneuran level of organization.

On the other hand, the Pyramidelloidea and the Euthyneura share synapomorphies of high significance, such as giant nerve cells, a rhinophoral and a lateral nerve and characters of the sperm (Haszprunar, 1988: 396–397; Healy, 1988a,b). Such proposed synapomorphies were in direct contrast to the originally assumed synapomorphies of the Allogastropoda, namely a shared gill position to the right of the dorsal ciliary tract, an acrembolic proboscis of distinct type (shifted position of buccal ganglia) and spermatophores (Haszprunar, 1985a). Meanwhile, however, pyramidelloids with a different position of the gills (Amathinidae; Ponder, 1987) and a mathildid with the usual placement of buccal ganglia (*Geganyia*; Haszprunar, 1985b) were described. This leaves the spermatophores with very low significance.

As a conclusion, I corrected my earlier opinion and regard the "Allogastropoda" now as a distinct grade rather than a clade. Within this grade, the Pyramidelloidea are placed closest to the Euthyneura, and both taxa represent a sister-group relationship.

CLASSIFICATION

In my approach, the final cladogram is a theorem of probability with very different degrees of likelihood in the various stem-lines of taxa. It is essential to note that a **reconstruction of phylogeny** should be translated into a classification, and not **the phylogeny** itself. In an attempt to base the classification on the same principle as the analysis (probabilities), the central taxa should reflect the highest degrees of certainty in the analysis. A similar point of view was made by Wiley (1979, 1981) in claiming to retain "important" taxa, which very often reflect stem-lines with high probabilities.

Evolutionary systematists often claimed the inclusion of the "anagenetic component" into the classification (e.g. Mayr, 1981). Taxa of high rank are interpreted as an expression of major evolutionary gaps. This array can be real if caused by fast adaptive radiations and a lack of intermediate forms. I interpret taxa of high rank as reflecting stem lines with very likely monophyly. This interpretation equals the distinction between apomorphy and plesiomorphy and gaps between character states (in a reconstruction). In this way, clado- and anagenesis are considered by correlating each with some probability.

Whereas many authors prefer Wiley's (1979, 1981) sequential method of classification, other cladists still use the dichotomic Hennigian way (e.g. Ax, 1984, 1987; Berthold & Engeser, 1987). I prefer the former, and regard my own proposal as a modification of Wiley's (1981) methodology.

Gauthier (1986) has proposed marking so-called "metataxa" (i.e. taxa, the holo- or paraphyletic status of which cannot be given at present) by an asterisk (taxon*). In combining my original mode of marking grades as "taxa" (Haszprunar, 1986) with Gauthier's (1986) ideas, I have more recently proposed to mark grades by asterisks (*taxa*) and to mark metataxa (e.g. *Architaenioglossa*, *Cerithiimorpha*) by a combination of asterisks and *sedis mutabilis* in the subtaxa (Salvini-Plawen & Haszprunar, 1987; Haszprunar, 1988). This enables a better conversation of a metataxon into an para- or holophyletic taxon upon addition of new data. At the time the study was finished, the Cerithioidea was an example of a metataxon. I regard Bieler's (1990) solution of omitting the Cerithioidea from the classification as less acceptable than my proposal of marking the taxon unequivocally.

PRESERVATION OF TRADITIONAL NAMES

In the earliest phase of my phylogenetic work (Haszprunar, 1985a,b), I frequently created new taxa of high rank. However, "nobody can hinder me to become wiser," and several of my friends (see Acknowledgements) have convinced me that preservation of traditional names is a better way. As outlined in Haszprunar (1988: 370), certain new taxa still appear necessary to present phylogeny unequivocally or to reflect taxa with high propabilities. I consider the Archaeogastropoda in its traditional, paraphyletic (orthophyletic) sense still useful in systematics, because in many cases only shells (and radulae) are available, which do not allow for a more specific classification. Thiele's Mesogastropoda is a paraphyletic group—it independently gives rise to both the Stenoglossa and Euthyneura—and therefore has been abandoned. I also regard the Neotaenioglossa (again paraphyletic) as a provisional construct which should be abandoned in the future.

CONCLUSION

I have responded Bieler's (1990) critique on the mode of my phylogenetic analysis on streptoneuran gastropods as follows:

(a) I have provided arguments against doing a maximum-parsimony analysis with equal weighting of characters. (b) I have presented examples of the character analysis and of placement of taxa to demonstrate the method used in the analysis. Proposed synapomorphies are considered as two-fold hypotheses with distinct degrees of likelihood. Accordingly the cladogram is regarded as a theorem of probability, and taxa of high rank are thought to reflect stem-lines of high certainty. (c) I have explained the use of certain taxa in the proposed classification.

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APPENDIX

Corrections of Haszprunar (1988)

- (1) p. 377: replace “McLean, 1987” by “McLean, 1988”.
- (2) p. 378/legend Fig. 1: Replace “Ponder, 1987” by “Ponder, 1988a”.
- (3) p. 381: So far as is known Truncatelloidea—Vitrinellidae have monopectinate gills (e.g. Bieler & Mikkelsen, 1988).
- (4) p. 389, p. 400/Table 2, p. 416: As recently outlined by Houbrick (1989), I have misinterpreted his earlier data on *Campanile symbolicum*, listing “eggs connected by chalazae” for this taxon. In fact, campanilid egg-mass connections resemble those found in the Epitoniidae. True chalazae are present in the Valvatidae, however.
- (5) p. 400/Table 2: A loss of teleoconch occurs also in numerous euthyneuran taxa.
- (6) p. 401/Table 2: Tubular salivary glands with ducts occur in patelloid Docoglossa (Patellogastropoda), but not in Lepetelloidea.
- (7) p. 401/Table 2: A cord-like visceral loop throughout its length is restricted to the Patelloidea and Nacelloidea (Neolepetopsidae?).
- (8) p. 401/Table 2: Eyes with a lens also occur in the Fissurellidae and Scissurellidae.
- (9) p. 413: Replace “Haszprunar, 1988” by “Haszprunar, 1989”.
- (10) p. 420: Bieler (1988) found some more diagnostic differences between Architectonicidae and Mathildidae.
- (11) p. 424/Fig. 5: Points 41 and 42 should be interchanged.
- (12) p. 428/Table 5a: The arrangement and subordination of “Superfamily Hot-Vent group A (*Melanodrymia*)” and “Superfamily Neomphaloidea” might appear to include them in the Neritimorpha. Judged from text (pp. 412–414) and phylogram (p. 424/Fig. 5), it should be clear that this is not the case, however.
- (13) p. 428/Table 5a: Change “Nacelloidea Lindberg, 1988” to “Nacelloidea Thiele, 1891”; “Helicinoidea Thompson, 1980” to “Helicinoidea Férrusac, 1822”; and

"Scissurelloidea McLean & Haszprunar, 1988" to "Scissurelloidea Gray, 1847." According to Ponder and Warén (1988) it should be "Ampullarioidea Gray, 1824"; "Janthinoidea Lamarck, 1810"; "Littorinoidea Gray, 1840"; "Tonnoidea Suter, 1913"; and "Pterotrachoidea Férrusac, 1821" should be replaced by "Carinarioidea Blainville, 1818."

(14) p. 430 Table 5d: The wrong (printer's error) ranking should be corrected so that N. N. ("Helicoida") becomes superior to Neritomorpha and N. N. ("Euhelicoida").

(15) p. 436: Mackie (1984) was missing in the reference list.

(16) The symposium-volume, "*Proso-branch phylogeny*," was published in late 1988, and there are differences between the published papers and the manuscripts and abstracts that were made available to me prior to

publication (Bieler, 1988; Healy, 1988b; Houbrick, 1988; Lindberg, 1988; Ponder, 1988; Ponder & Warén, 1988). For example, Ponder's (1988) "Cingulopsoidea Fretter & Patil, 1958" was not included in my classification, for nomenclatorial corrections; see (13).

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